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The hosts of *Ophion luteus* (Linnaeus) (Hymenoptera, Ichneumonidae, Ophioninae) in Europe

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Abstract

A widespread European nocturnal ichneumonid, *Ophion luteus*, is shown to be a parasitoid of at least two species of noctuid moth, *Agrotis exclamationis* and *A. segetum*, probably most frequently a parasitoid of the former. The taxonomy, nomenclature and diagnostic features of this species are discussed. Possible explanations for a spring-flying generation, usually referred to as the '*distans*' morph, are discussed.

Keywords

Host-parasitoid, rearing, Lepidoptera, Noctuidae, Noctuinae

Introduction

In Europe, *Ophion luteus* (Linnaeus) is a widely distributed, often common, nocturnal ichneumonid, and a conspicuous visitor to light traps in August and September. But despite its near ubiquity in Britain (and probably much of north-west Europe) (Brock 1982; Natural History Museum and National Museums of Scotland collections), its biology has remained almost entirely unknown. Establishing the hosts of *O. luteus* is of interest because it is such a widespread (Fig. 1) and often common species, yet is one of very few ophionines that had not been reared in Britain. Population modelling work

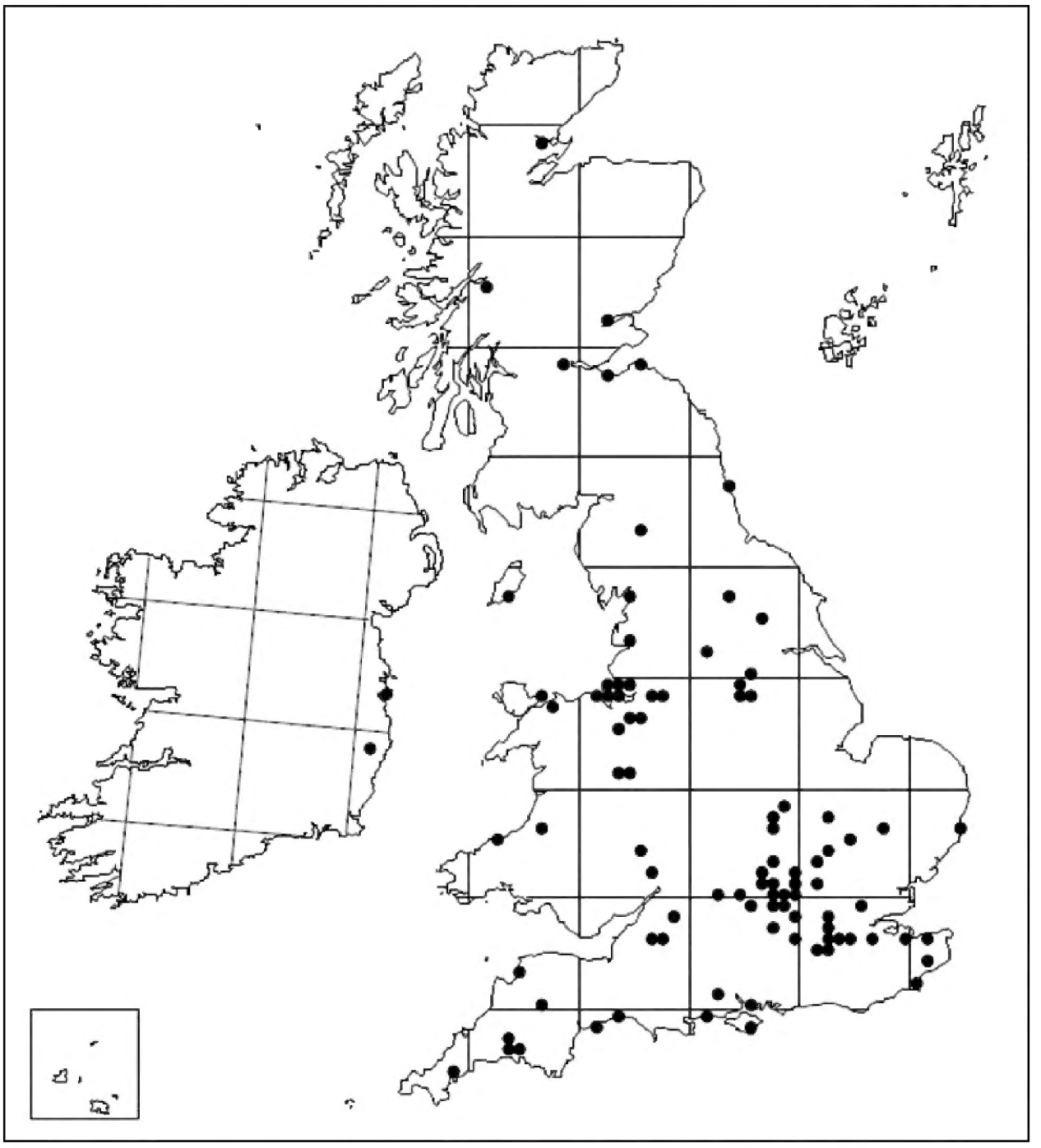

Figure 1. Preliminary distribution map of *Ophion luteus* in Britain and Ireland (Northern Isles displaced southwards), based on 475 occurrence records held in the database of the Nocturnal Ichneumonoidea Recording Scheme; note that many specimens in BMNH and NMS have not yet been databased and this map is presented only to give an impression of the range of the species, bearing in mind bias in coverage and omissions. Map plotted using DMAP, developed by Alan Morton (www.dmap.org).

in Finland has appeared to implicate parasitism by *O. luteus* as the cause of population cycles of boreal *Xestia* spp. (Noctuidae: Noctuinae) (Várkonyi et al. 2002), although *O. luteus* has never been reared from *Xestia*, neither in the wild nor by experimental exposure.

As Brock (1982) had suggested that the usual host of *O. luteus* is a "noctuid larva of such frequent occurrence that it is seldom reared by lepidopterists", GRB and MRS surmised that *Agrotis exclamationis* (Linnaeus) (Noctuidae: Noctuinae), the Heart & Dart, must be a good candidate for the usual host of *O. luteus*, given its wide distribution and suitable phenology. *Agrotis exclamationis* flies mainly from May to July, with well-grown larvae occurring in late summer to early autumn before overwintering

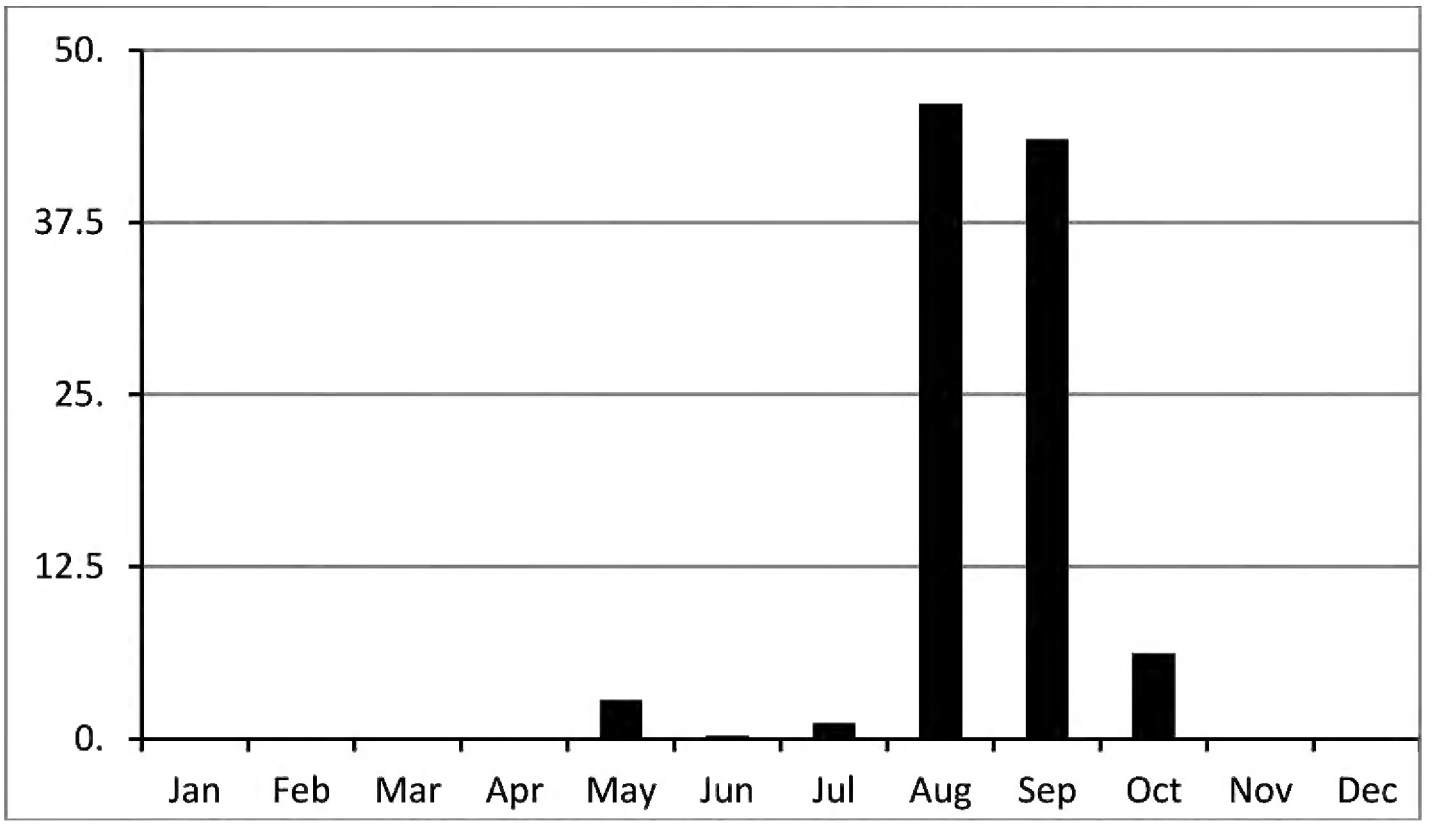

Figure 2. Phenology of adult *Ophion luteus* in Britain (percentages per month of 887 specimens from the Nocturnal Ichneumonoidea Recording Scheme database). Note the tiny May emergence.

fully fed to pupate the following spring. Adult *O. luteus* specimens have been collected in Britain mainly (90% of specimens seen) in August and September (Fig. 2) which would mean they are adult at a time coincident with suitable *A. exclamationis* larval hosts. Ophioninae almost always oviposit into well-grown Lepidoptera larvae (e.g. Price 1975; Vickery 1929; MRS pers. obs., see below) and many of the British species attack Noctuidae (Brock 1982 and collections of NMS); but larvae of common noctuids feeding partly subterraneously, such as *A. exclamationis*, are not often reared by lepidopterists. An opportunity to rear *O. luteus* (including experimental exposure to the parasitoid) arose when GRB collected several final instar larvae of *A. exclamationis* at night on 10.x.2012 in his garden, in Aldbury, Hertfordshire, England (51°47'59"N, 0°35'59"W), where *O. luteus* is frequent at the light trap. While these caterpillars were being reared, MRS and HS coincidentally reported further rearing records for *O. luteus*. The rearings by HS took place as a result of large populations in 1976 and some subsequent years of *Agrotis segetum* (Denis & Schiffermüller) and, to a lesser extent, *A. exclamationis* in Saxony and other regions of Central Germany (specimens retained from Dübener Heide and Eisleben), where the larvae (particularly of *A. segetum*) caused significant damage to crops.

Materials and methods

Specimens are deposited in the Natural History Museum, London (BMNH), National Museums of Scotland (NMS) and the Heinz Schnee collection (HSC). Rearing by

Table 1. Rates of parasitism of two *Agrotis* spp. by *Ophion luteus* in Central Germany.

Agrotis exclamationis			*Agrotis segetum*		
Year	**No. larvae**	**Parasitism (%)**	**Year**	**No. larvae**	**Parasitism (%)**
1976/7	138	0.7	1976/7	585	0.5
1977/8	100	11	1979/80	115	0.9
1981/2	48	2.1	1981/2	75	1.3
1983/4	64	7.6	1983/4	200	0.5
1984/5	44	6.8	1984/5	69	4.3
1985/6	52	7.7	1986/7	148	0.7
1990/1	58	1.7	1988/9	388	0.3
			1991/2	90	1.1

GRB of *A. exclamationis* larvae collected in the wild in their final instar was carried out in a shed at ambient temperatures throughout the winter, with livestock brought indoors, to a shaded environment, in the summer. Two wild-collected adult female *Ophion luteus* were fed on diluted honey and six final instar *A. exclamationis* larvae were exposed to them overnight, around 10.x.2012. *Ophion luteus* adults were introduced to large tubes containing single *A. exclamationis* larvae in the evening and observed from about 20:00-22:00. The two *O. luteus* were then separately left overnight with multiple *A. exclamationis*. In Germany, larvae of *A. exclamationis* and *A. segetum* were collected in October and November over several years (see Table 1), mainly from potato and sugar beet fields but also from corn and carrot. Larvae were reared individually in Petri dishes under long daylight conditions (18 hours light / 6 hours darkness) until emergence of adult moths, parasitoid larvae or death of the larvae. Parasitoid cocoons were over-wintered outdoors. Photographs of specimens were taken with a Canon EOS 450D digital camera attached to a Leica MZ12 stereomicroscope and partially focused images were combined using Helicon Focus v. 4.80 software. A photograph of the early cocoon was taken with a Samsung Galaxy SII mobile phone.

Results and discussion

The *Agrotis exclamationis* larvae collected in Aldbury in October 2012 were exposed to *O. luteus* females; during the period of observation, from about 20:00-22:00. *Ophion luteus* females paid no attention to the *Agrotis* larvae, even when walking over them. In light of the subsequent parasitoid emergence, they could already have been parasitized, or oviposition may have subsequently occurred in the dark, when they were not under observation. It proved difficult to overwinter the *A. exclamationis* larvae, which bury themselves in soil but are periodically restless. Most larvae succumbed to fungi but one survived the winter. On 19.iv.2013, it was found that a large parasitoid larva had emerged from this, probably prepupal, caterpillar and had begun to spin a cocoon below the host remains. Cocoon formation took about seven days, with the cocoon

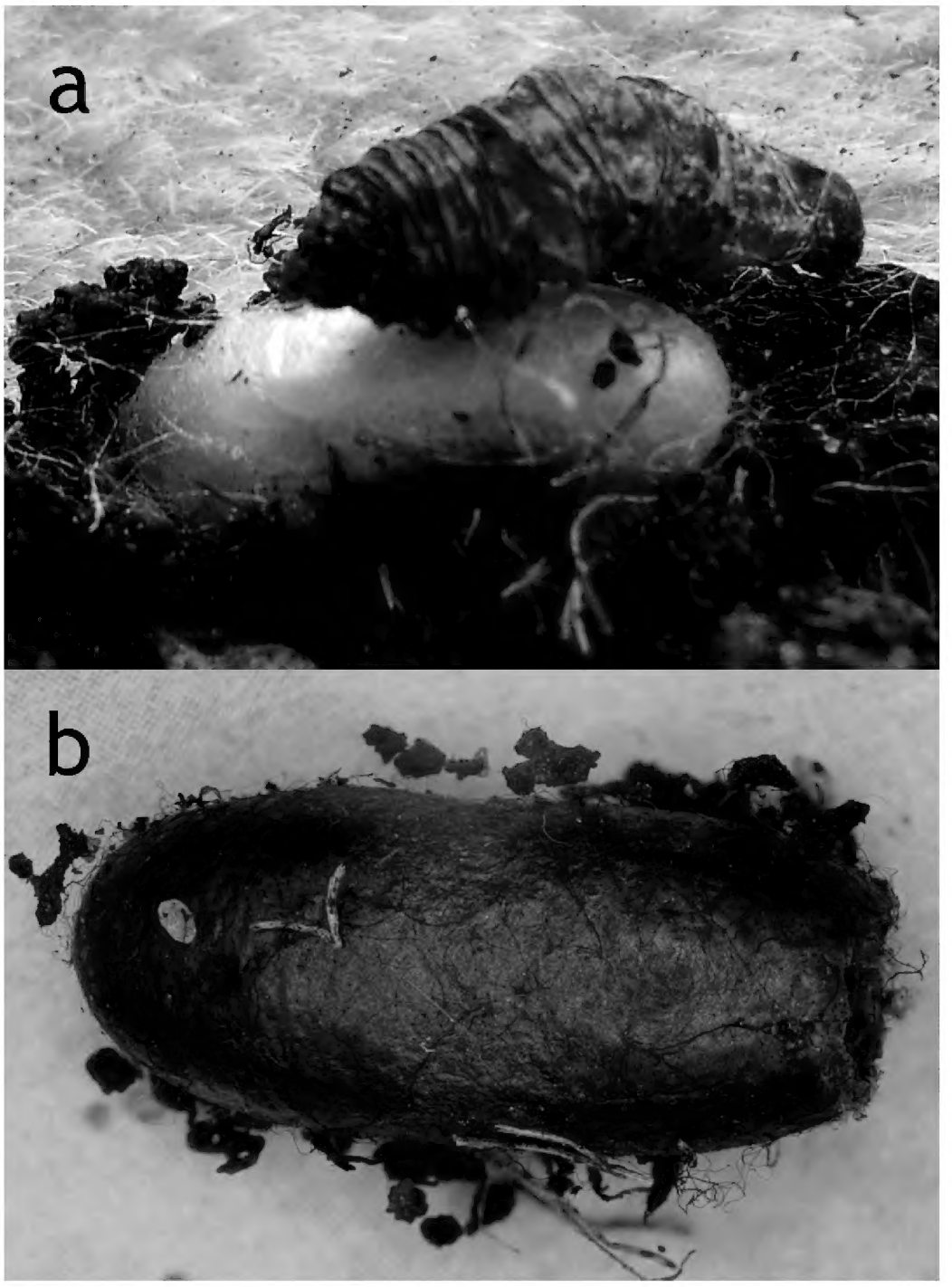

Figure 3. Cocoon of *Ophion luteus* ex *Agrotis exclamationis* (Aldbury, Herts.); **a** early stage in cocoon formation, 20.iv.2013 **b** same cocoon after emergence of adult *O. luteus*.

initially composed of loose, white silken threads (Fig. 3a) but gradually darkening and taking on the characteristic appearance of an *Ophion* cocoon, dark brown, slightly paler centrally (Fig. 3b). An adult female *O. luteus* emerged in the night of 2-3.ix.2013 (specimen deposited in BMNH). At around this time, *O. luteus* were regularly caught in GRB's light trap.

At about the same time as this specimen was pupating, MRS identified a female *O. luteus* reared from a fully grown *Agrotis* ?*vestigialis* (Hufnagel) larva, or prepupa, collected from under moss at Braunton Burrows, North Devon (SS4437) on 8.v.2007 (coll. B.P. Henwood) (specimen in NMS). The exact dates of cocoon formation and emergence of the adult parasitoid are not recorded, but were later in 2007.

HS also reported his previously unpublished rearing records from 1976–1992, when he reared 43 *O. luteus* from both *Agrotis exclamationis* and *A. segetum* field-col-

lected larvae in Germany (Table 1) (12 reared *O. luteus* specimens deposited in HSC). Unlike GRB's rearing, the *O. luteus* larvae in HS's rearings all emerged from their host larvae in the year of collection, although it should be noted that these emergences took place under unnatural light conditions, as detailed in Materials and Methods. HS also found some *Ophion* cocoons in the soil in November; however, emergence of these *O. luteus* adults was almost invariably between July and early September in the following calendar year, except for two that emerged in May. The phenology of both hosts and *O. luteus* may differ in Germany, at least in particularly warm years (such as 1977) but in Britain, *A. exclamationis* usually overwinters as a prepupa in the soil, pupating the following spring.

Host records for *O. luteus* in the literature cover a very wide range of Lepidoptera across ten families, including many noctuids, and even a tenthredinid sawfly (Yu et al. 2012). Most can be dismissed out of hand, especially as in the past almost any large yellowish ichneumonid was liable to be referred to *O. luteus*. However, Meyer's (1927) and Győrfi's (1943, 1944) references to, respectively, *Agrotis segetum* and *A. vestigialis* as hosts are, in retrospect, entirely plausible.

Almost all *O. luteus* records from GRB's Nocturnal Ichneumonoidea Recording Scheme are from August and September (and into early October) (Fig. 2), which is when large larvae of *A. exclamationis* and some other *Agrotis* species are available. However, as discussed by Brock (1982), there is a distinct, though rarely collected, cohort of apparent *O. luteus* on the wing in May. These specimens are typically smaller than normal *O. luteus*, with fewer antennal flagellomeres and more buccate heads (there is a distinct ocellar-ocular space and the temples are long in dorsal view). These have informally been referred to as the '*distans*' morph. The taxonomy of this morph is rather complex; the lectotype of *Ophion distans* Thomson, 1888 is very similar to that of *Ophion luteus* (Linnaeus, 1758) (Brock 1982) so, although this spring generation is informally called the '*distans*' morph, if there were found to be two species (spring and autumn-flying) then the '*distans*' morph would actually take the name *Ophion luteus*, with the autumn generation taking the next available name, *Ophion slaviceki* Kriechbaumer, 1892 (Brock 1982). However, Schwarzfeld et al. (submitted) have found that all British specimens of *O. luteus* sequenced for Cytochrome Oxidase I, including two '*distans*' specimens collected in May, cluster together as apparently one monophyletic species.

Brock (1982) reports that *O. luteus* of the '*distans*' form have been reared from *Ochropleura praecox* (Linnaeus) (Noctuidae: Noctuinae) on sand dunes, based on specimens in Claude Morley's collection, but the location of these specimens is now unknown. Four specimens in BMNH, reared by Claude Morley but with no host names given, seem to be '*distans*' although three of these have atypical mandibles, having the acute internal angle between the teeth that is a feature of most *Ophion* species other than *O. luteus*. The lectotype of *Ophion luteus*, and other '*distans*' specimens, have mandibles typical of the common and widespread form of *O. luteus*.

Agrotis exclamationis can have a small second brood (as occurred in 2013 in southern England), and it is plausible that the early-flying '*distans*' form results from late summer or autumn-pupating host individuals, with the parasitoid's early cocoon for-

mation triggered by hormonal changes in the host. These could give rise to adult *O. luteus* emerging in the late spring. However's HS's autumn-cocooning *O. luteus* are of the usual, autumn-flying morphology, including the two specimens that emerged in May (possibly as a result of unnatural rearing conditions). There are also, perhaps more pertinently, closely related dune-inhabiting noctuid species with this different phenology. Both factors mean that alternative hosts may be available in some areas for an early summer brood of *O. luteus*.

There are no reliable rearing records of *O. luteus* from any *Xestia* species. *Xestia* spp. and *O. luteus* have non-synchronous life cycles in Britain, with fully-grown *Xestia* larvae unavailable at the time for oviposition by *O. luteus*. The available evidence is that *O. luteus* is a parasitoid of *Agrotis* larvae, contrary to Várkonyi et al. (2002). Várkonyi et al.'s (2002) population modelling of boreal *Xestia* species implicitly assumes that *O. luteus* is a parasitoid attacking early instar host larvae, switching between two cohorts of *Xestia* spp. (which have a two year life history at high latitudes), because *Xestia* are not fully grown in Finland when *O. luteus* is on the wing. Várkonyi et al. (2002) also report *O. luteus* rearings from *Euxoa* species, which over-winter as small larvae, and use this as evidence for *O. luteus* ovipositing in small larvae of *Xestia* spp. This is contrary to our findings, as *O. luteus* adults are only on the wing when their *Agrotis* hosts are well-grown, and oviposition in young larvae would be unique within the genus. MRS has experience of rearing at least ten British *Ophion* species, always from Lepidoptera larvae collected as late (probably final) instars and never from larvae collected young, which he collects as often as possible for the sake of rearing Microgastrinae and Rogadinae (Braconidae) that kill hosts young. Furthermore, common *Xestia* species are easily collected as larvae in Britain, and have repeatedly been reared in large enough numbers for it to be implausible for regular parasitism by *O. luteus* to have been overlooked in Britain. There is a possibility that the Scandinavian and British specimens identified as *O. luteus* represent separate species (G. Várkonyi pers. comm.) although there has been no published evidence to support this. Three specimens of *Ophion* reared from *Euxoa* in Scandinavia have been identified as *O. luteus* by J.P. Brock (Brock, pers. comm.), which again raises the question of whether *O. luteus* as currently defined actually conceals more than one species, assuming that the host identification as *Euxoa* is correct (these specimens were not available to us). Despite these outstanding questions, we can now say that the common European species that we call *Ophion luteus* is most likely a frequent parasitoid of the noctuid *Agrotis exclamationis* and congeners and the hosts of any cryptic species within this complex should be found within noctuid larvae that are almost certainly late instars at the time the *Ophion* species is/are on the wing.

Identification of *Ophion luteus*

As with many species of *Ophion*, *O. luteus* is predominantly testaceous/pale orange and many *Ophion* in collections (and online images) are misidentified as *O. luteus*, which has generally been used as a catch-all name. However, Brock (1982) clarified the

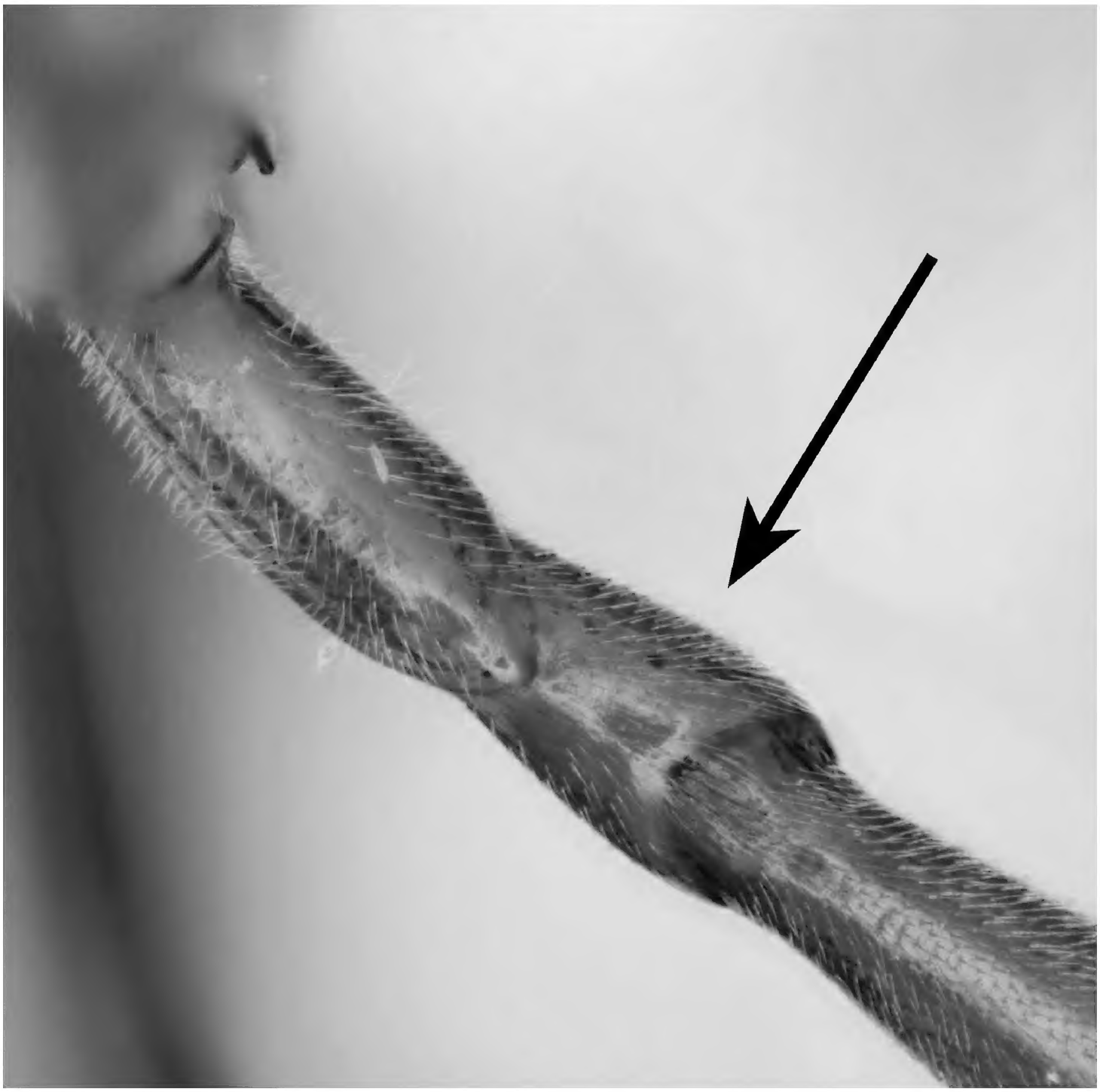

Figure 4. Hind leg of *O. luteus* with arrow pointing to trochantellus (leg parts as follows from top left to bottom right: coxa, trochanter, trochantellus, femur).

identification of *O. luteus* in his comprehensive key to the British *Ophion* species. This key can be difficult to use (because they are on the whole difficult species to identify), but *O. luteus* is usually relatively straightforward to identify. With the exception of very aberrant specimens, such as those reared by Morley (see above), *O. luteus* (including all specimens of the "ordinary" form and most of the "*distans*" form) can be identified by the combination of the long hind trochantellus (Fig. 4) and the usually characteristic mandibles (Fig. 5), which have simply tapered internal edges to the mandibular teeth, lacking internal angles at the base of the teeth (compare with the mandible of *Ophion crassicornis* Brock in Fig. 6), and often show considerable wear. Very occasionally, *Ophion crassicornis* may have very worn mandibles too, when the internal angles of the teeth are then not visible. Additional useful recognition features for *O. luteus* are the strongly sinuous fore wing vein *Rs* and the very short ramellus on fore wing vein

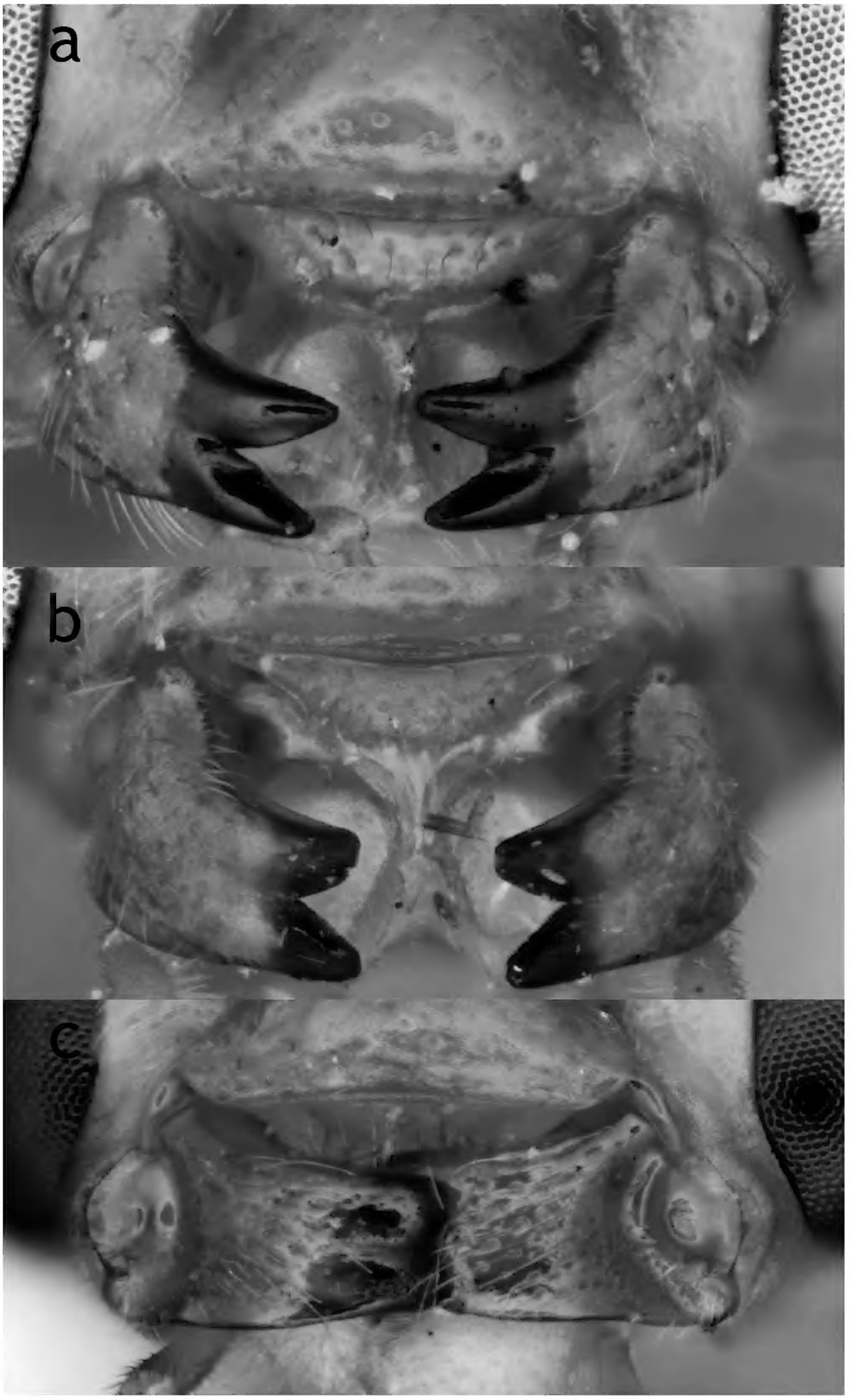

Figure 5. Mandibles of female *O. luteus*, showing differing degrees of abrasion; **a** Bath University, 14.x.2005 (coll. D. Watts) **b** Silwood Park, Berks., 16.viii.2000 (coll. G.R. Broad) **c** Aldbury, Herts., 13.ix.2013 (coll. G.R. Broad); all specimens in BMNH.

Figure 6. Mandible of *Ophion crassicornis* (Westcott, Bucks., 21.v.2009, coll. D. Wilton, BMNH).

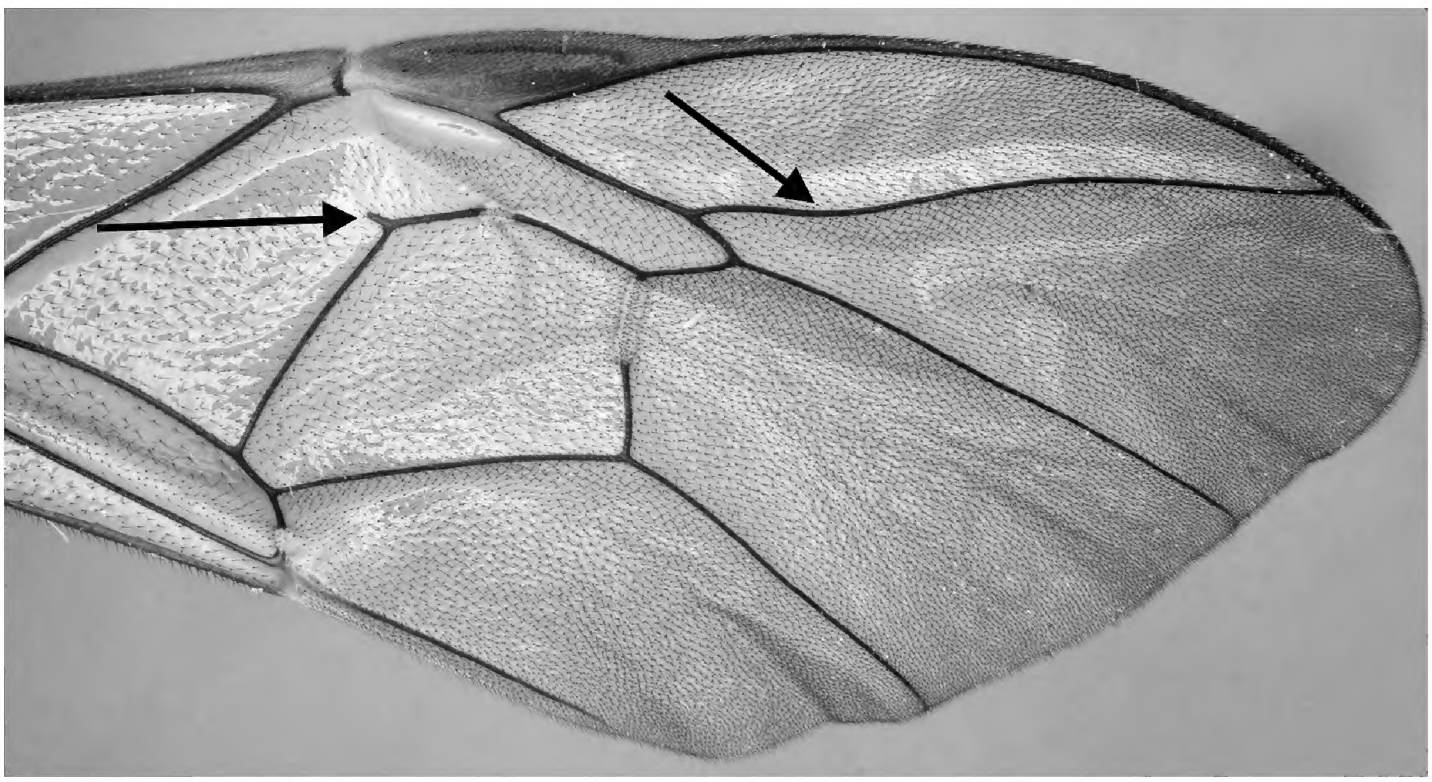

Figure 7. Fore wing of *Ophion luteus* (Aldbury, Herts., 29.ix.2012, coll. G.R. Broad) with arrows pointing to the ramellus (left) and vein *Rs* (right).

1*m-cu* (Fig. 7), together with the sparsely punctate mesopleuron (densely punctate in *O. crassicornis*) and very weak median longitudinal carinae on the propodeum (strong centrally in *O. crassicornis*). The mandibular teeth of *O. luteus* are frequently granulose in sculpture and the teeth may be worn down; the range of mandibular abrasion is shown in Fig. 5. Presumably the mandibles are abraded when the *Ophion* adults emerge from the soil, as this is seen in males as well as females and the mandibles of our reared specimens are unabraded and shiny. Some females have particularly strongly abraded mandibles (Fig. 5c), which still requires explanation – perhaps the soil that the adults need to tunnel through from their subterranean cocoons can become very strongly compacted and hard following a dry summer period, but males in general do not exhibit such extreme wear. *Agrotis* larvae are found above the soil surface at night, when they are presumably attacked by *O. luteus*, and *O. luteus* does not exhibit any modifications typically seen in ichneumonoids parasitising soil-inhabiting Lepidoptera, such as robust legs and short antenna.

Acknowledgements

Mike Fitton provided access to the lectotype of *Ophion luteus* in the collections of the Linnean Society. B. P. Henwood kindly donated his reared *O. luteus* to MRS for identification and deposition in NMS. We are grateful for the constructive criticism offered by the small army of reviewers.

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